

# Geometric interpretation of phyllotaxis transition

Takuya Okabe

Faculty of Engineering, Shizuoka University, 3-5-1 Johoku, Hamamatsu 432-8561, Japan

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## Abstract

The original problem of phyllotaxis was focused on the regular arrangements of leaves on mature stems represented by common fractions such as  $1/2$ ,  $1/3$ ,  $2/5$ ,  $3/8$ ,  $5/13$ , etc. The phyllotaxis fraction is not fixed for each plant but it may undergo stepwise transitions during ontogeny, despite contrasting observation that the arrangement of leaf primordia at shoot apical meristems changes continuously. No explanation has been given so far for the mechanism of the phyllotaxis transition, excepting suggestion resorting to genetic programs operating at some specific stages. Here it is pointed out that varying length of the leaf trace acts as an important factor to control the transition by analyzing Larson's diagram of the procambial system of young cottonwood plants. The transition is interpreted as a necessary consequence of geometric constraints that the leaf traces cannot be fitted into a fractional pattern unless their length is shorter than the denominator times the internode.

**Keywords:** Schimper-Braun's law, *Populus deltoides*, Fibonacci numbers, golden ratio, phyllotaxy

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## 1. INTRODUCTION

The spiral arrangement of leaves on a stem, phyllotaxis, is represented by the fraction of the circumference of the stem traversed by the spiral in passing from one leaf to the next. Braun and Schimper discovered that leaves are lined up in ranks parallel to the stem so that the fraction is literally represented by a common fraction (Braun (1835)). In a  $3/8$  phyllotaxis, for instance, every eighth leaf comes over one below it after three turns of the spiral, so that eight straight ranks are visible along the stem (Fig. 1). To this day, the following list of the most common fractions has been circulated in books and websites for non-specialists;  $1/2$  for elm, lime and linden,  $1/3$  for beech and hazel,  $2/5$  for oak, cherry, apple, holly and plum,  $3/8$  for poplar, rose and pear,  $5/13$  for almond, etc. Such correspondence tables seem to have existed already in the middle of the nineteenth century (Henfrey (1870)). Sometimes willow is listed in  $5/13$  (Coxeter (1961)) and sometimes in  $3/8$  (Adam (2006)). As a matter of fact, it had been remarked since early times that even an individual plant sometimes makes transitions between different fractions (Braun (1835)). Therefore, the phyllotaxis fraction is not a determined characteristic of each species. Most notably, Larson (1980) has revealed the manner in which the vascular system is rearranged through the phyllotaxis transition by mapping arrangement of the leaf traces, the portion of vascular bundles of leaves that resides in the stem (Fig. 2). By contrast, it has been commonly accepted that the arrangement of leaf primordia in the bud or at the shoot apical meristem does not conform to any fractional number;

primordia do not appear as radial rows. The angular divergence between successive primordia stays close to a unique "ideal" angle of  $137.5^\circ$ , which is the golden mean  $0.3820$  of  $360^\circ$  (Church (1920); Richards (1951)). The golden mean is a mathematical limit of the sequence of the above fractions. Much attention has been paid to mathematics of these numbers and to mechanisms of leaf primordia formation by which the ideal angle is achieved and regulated (Adler et al. (1997)). In contrast, the phyllotaxis transition has been left unexplained without attracting interest from researchers. The fractional phyllotaxis and the phyllotaxis transition are two sides of the same problem. A key point noted in the present study is that phyllotaxis in the bud changes *continuously* whereas phyllotaxis on the mature stem changes *stepwise*. Evidently, the arrangement of primordia at the apical growing point must be a determining factor of leaf arrangement on the mature stem. But what causes the transition from  $2/5$  to  $3/8$ , for instance? There must be another factor. Larson (1980) has suggested that the transition is programmed in the plant to occur at specific stages of ontogeny. In another view, phyllotaxis of primordium formation and vascularization are controlled by some higher-level system (Romberger et al. (1993)). Kuhlemeier (2007) remarks that virtually nothing is known about the molecular mechanisms that underlie the transitions between different spiral systems (e.g.  $3/8$  to  $5/13$  patterns), except that larger meristems seem to have higher Fibonacci numbers. The present paper aims at pointing out that this phenomenon is consistently explained by considering geometry of growing leaf traces. By means of a full quantitative analysis, which surely is not standard in this field of research, it is shown (1) that the positions of the phyllotaxis transition are located based

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Email address: ttokabe@ipc.shizuoka.ac.jp (Takuya Okabe)



Figure 1: A young poplar in a  $3/8$  phyllotaxis with eight vertical ranks of leaves.

on the angular positions at which leaf traces exit from the vascular cylinder and (2) that the phyllotaxis transition is caused as a necessary consequence of change in size of leaf traces relative to internode length.

A caveat: this paper deals with the mechanism of the phyllotaxis transition in spiral systems. Although a common keyword of “phyllotaxis” may suggest, it should not be confused with mechanisms of phyllotactic primordium formation, for which considerable advances have been made over the last decade (Kuhlemeier (2007)). Models of the latter category deal with continuous changes of apical meristems, while they are not concerned with the fractional expression of a phyllotactic pattern.

## 2. MATERIAL AND METHODS

The analysis is based on a diagram of the procambial system of a cottonwood plant (*Populus deltoides*) reconstructed by Larson (1980), which is reproduced in Fig. 2. The vascular cylinder is displayed as if unrolled and laid flat. The ordinate is the leaf plastochron index (LPI) for numbering leaves. Each leaf has three traces: central, right and left traces exit the vascular cylinder at positions denoted by symbols  $\times$ ,  $\triangle$  and  $\blacktriangle$ , respectively. For more details, see Larson (1980) and references cited therein.

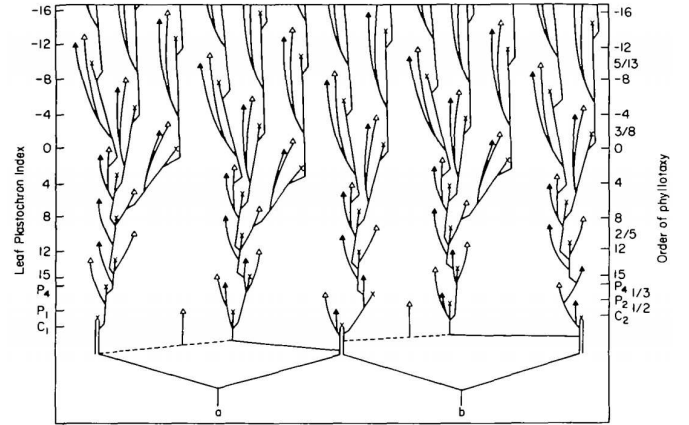


Figure 2: Diagram of the procambial system of a typical cottonwood plant compiled by Larson (1980). The vascular cylinder is displayed as if unrolled and laid flat. The ordinate is the Leaf Plastochron Index (LPI) for leaves, whereas the abscissa corresponds to the angular coordinate in a full turn about the stem axis. Each leaf is entered by three traces; a central ( $\times$ ), right ( $\blacktriangle$ ), and left ( $\triangle$ ) traces. Phyllotaxis orders,  $1/2$ ,  $1/3$ ,  $2/5$ ,  $3/8$  and  $5/13$ , are indicated by the right vertical axis.

By virtue of the convention to take LPI as the ordinate, the vertical scale of the diagram is normalized such that differences in height between two successive leaves, or internodes, are a unit of length in the vertical direction. Therefore, the vertical component of a line segment in Fig. 2 represents not its actual length but an effective length relative to the internode length, namely the length measured in internode units. Accordingly, vertical lengths of the leaf traces in internode units are directly evaluated by applying a digitizing ruler to the diagram. The lower end points of right and left traces are located without ambiguity, for they are connected to other types of traces. Lengths of central traces are fixed by decomposing the whole pattern into clusters consisting of three adjacent traces, the right trace of leaf  $n$ , the central trace of leaf  $n + 2$  and the left trace of leaf  $n - 1$ , where  $n$  for LPI is an integer. For illustration purposes, the clusters from  $n = 0$  to 7 are shown in Fig. 5. The length of the leaf traces thus obtained is plotted against LPI in Fig. 3, where reading errors are of the order of an internode at most. On the other hand, divergence angles are evaluated from the horizontal, angular coordinates of the exit points of the leaf traces denoted by the symbols. Evaluated angles show rhythmic, systematic variations around the “ideal” angle, which are typically observed in a quantitative analysis (Okabe (2012a)). The systematic variations, which are correlated with the angular positions, are suppressed apparently by deleting from the diagram a blank rectangular strip of a narrow width along the left ordinate. The width of the strip is determined so as to minimize the standard deviation of divergence angles for ten youngest central traces (LPI less than  $-6$ ). Results for the divergence angle thus corrected are shown in Fig. 4. The width

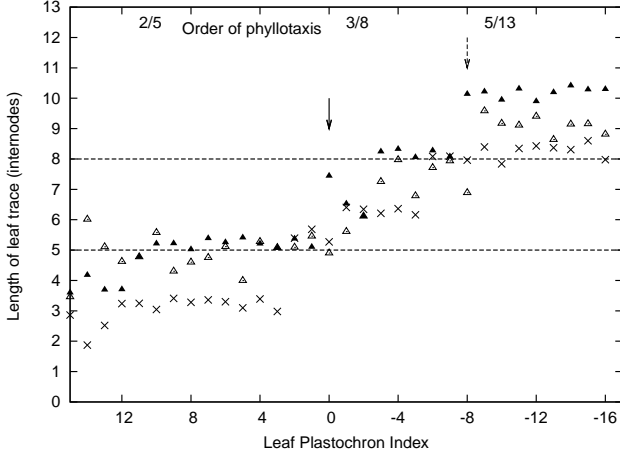


Figure 3: Vertical length of leaf traces in Fig. 2 is plotted against the Leaf Plastochron Index. Orders of phyllotaxis, 2/5, 3/8 and 5/13, are denoted at the same position as indicated in Fig. 2. See Fig. 2 for trace designations. The phyllotaxis transitions from 2/5 to 3/8 and from 3/8 to 5/13 are caused by the traces indicated by a solid arrow and a dashed arrow, respectively. Horizontal dashed lines at 5 and 8, separating the different phyllotaxis regimes, are drawn for reference sake (see Results and Discussion).

ratio of the deleted strip is 0.023, whereby the standard deviation of the divergence angle is suppressed from  $4.2^\circ$  to  $0.89^\circ$ . The correction is made for ease of understanding implications of Fig. 4. It does not affect the results discussed below qualitatively.

### 3. RESULTS

Results in Fig. 3 indicate that the three traces grow in length steadily all alike. This behavior is consistent with other quantities reported by Larson (1980). According to Fig. 3, three traces at LPI 2 have almost the same length of about five internodes. This means that the traces at LPI 2 extend down to the height of LPI 7 (see Fig. 2). As indicated by the right ordinate of Fig. 2, the phyllotaxis order fraction changes from 2/5 through 3/8 to 5/13 as we climb up the stem, or as LPI decreases. The order fractions are indicated at the top of Fig. 3 at the same LPI coordinates as in Fig. 2 by Larson (1980). Horizontal dashed lines at five and eight internodes in Fig. 3 are drawn to separate regimes of different phyllotaxis orders (see below).

Divergence angle between the leaf traces at LPI  $n$  and  $n+1$  is plotted against LPI  $n$  in Fig. 4. The inset shows the angle between the central traces at LPI  $n$  and  $n+5$ , that is, the net angle of inclination of 5-parastichies. The angle should become zero, 45 and 28 degrees for 2/5, 3/8 and 5/13 ideal patterns, respectively; for instance, the ideal angle for 3/8 is  $360 \times 3/8 \times 5 = 360 \times 2 - 45$ , which is congruent to  $-45$ . The inset of Fig. 4 clearly indicates stepwise transitions between the three distinct fraction regimes. Thus, the positions of the phyllotaxis transition are located based on the exit points, or the bases, of the leaf traces, i.e., with-

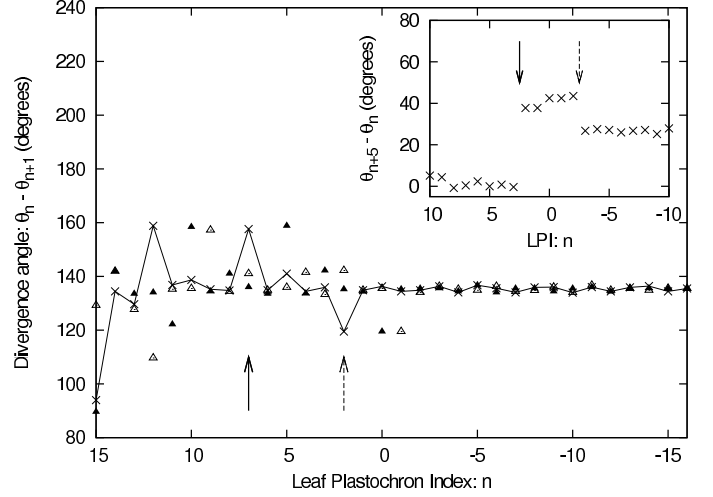


Figure 4: Divergence angle between the traces at LPI  $n$  and  $n+1$  is plotted against LPI  $n$ . See Fig. 2 for trace designations. The inset shows the angle between the central traces at LPI  $n$  and  $n+5$ : for ideal patterns of 2/5, 3/8 and 5/13 orders, it should be zero, 45 and 28 degrees, respectively. The positions at which the phyllotaxis transitions from 2/5 to 3/8 and from 3/8 to 5/13 occur are indicated by solid and dashed arrows, respectively.

out inspecting internal changes in the vascular structure. This crucial property for us is brought to light probably because the subject plants are grown under controlled uniform conditions (Larson (1980)).

The cause of the transition is traced back by close inspection based on the quantitative results. The transition from 3/8 to 5/13, indicated by a dashed arrow in the inset of Fig. 4, is caused by an irregular decrease of divergence angle at LPI 2, which therefore is also indicated by a dashed arrow in the main figure. Similarly, a solid arrow in the inset indicates the transition from 2/5 to 3/8, which is ascribed to an increase of divergence angle at LPI 7, a solid arrow in the main figure.

In connection with the latter transition, it is worth a remark that divergence angle in the 2/5 phyllotaxis regime is not held at an ideal constant value of  $144^\circ$  ( $360 \times 2/5 = 144$ ). This means that five ranks (orthostichies) of a real 2/5 pattern is not equally spaced. According to Fig. 4, two full turns ( $360^\circ \times 2$ ) of the 2/5 pattern is divided roughly into unequal parts of  $140^\circ \times 4 + 160^\circ \times 1$ , instead of a regular spacing with  $144^\circ \times 5$ . The figure shows that the irregular shift at LPI 7 is shared with LPI 12. This is just as expected for the 2/5 arrangement ( $7 + 5 = 12$ ). Similarly, a cycle of  $360^\circ \times 3$  of a 3/8 pattern is divided into  $137^\circ \times 7 + 120^\circ \times 1$ , as indicated by the dashed arrow. Thus, the quantitative analysis reveals that divergence angle *on a stem* is a secondary property, as it is very unlikely that the exceptional angles of  $160^\circ$  and  $120^\circ$  are intrinsic to the plant. Accordingly, the pattern of Fig. 2 is to be viewed as a result of secondary processes.

The final step is to identify the cause of the irregular shift in divergence angle. For brevity, let the central ( $\times$ ),

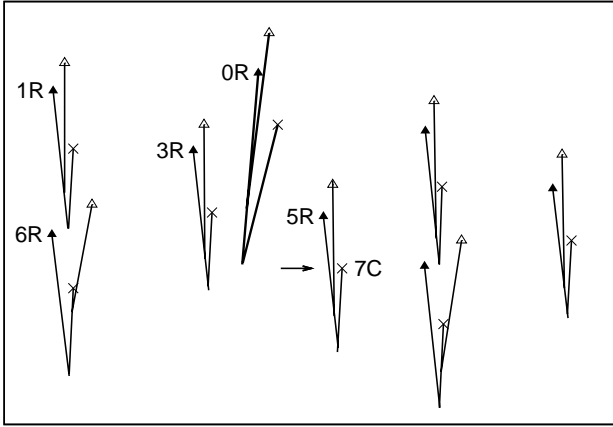


Figure 5: A schematic excerpt from Fig. 2 near the transition from  $2/5$  to  $3/8$ . The right trace at LPI 5 is denoted as 5R, and 7C signifies the central trace at LPI 7. According to Fig. 4, the traces 5R and 7C are shifted slightly to the right as compared to the preceding (lower) traces. This figure shows that the shift (solid arrow) is caused by a longer trace 0R intervening between 3R and 5R, thereby the transition is initiated. If the length of 0R were shorter than five internodes, 0R should have been aligned with 5R to keep the  $2/5$  order, as the preceding 1R is with 6R.

right ( $\blacktriangle$ ) and left ( $\triangle$ ) trace of LPI  $n$  be denoted as  $nC$ ,  $nR$  and  $nL$ , respectively. At the transition from  $2/5$  to  $3/8$ , the irregular shift of 7C (solid arrow) is accompanied by 5R on the right side (Fig. 4). Inspection of Fig. 2 reveals that this collective shift is caused as a result of 0R intervening between 3R and 5R. This is illustrated in Fig. 5, a schematic excerpt from Fig. 2. For this reason, the trace 0R is indicated by a solid arrow in Fig. 3 as the very cause of the phyllotaxis transition from  $2/5$  to  $3/8$ . A horizontal line at five is drawn in Fig. 3 to indicate that 0R interferes with 5R if only the former length exceeds  $5 - 0 = 5$  internodes (cf. Fig. 5). Indeed, the filled triangle at the solid arrow in Fig. 3 lies well above the horizontal line at five internodes. Similarly, the trace causing the transition from  $3/8$  to  $5/13$  is indicated by a dashed arrow in Fig. 3, where the upper horizontal line at eight is drawn as a threshold length for the transition.

#### 4. DISCUSSION

The trace length represented in internode units is an important geometric factor as it imposes constraints on possible fractional patterns to be realized (Okabe (2011, 2012b)). The geometric effect invoked in interpreting the above results is schematically illustrated in Fig. 6. During growth of the shoot apex, the precursor of the vascular system associated with a leaf primordium develops to become the leaf trace (Romberger et al. (1993)). Both lengths of the leaf trace and internode change continuously during growth. In this view, the phyllotaxis order to be realized on the mature stem is determined depending on the trace

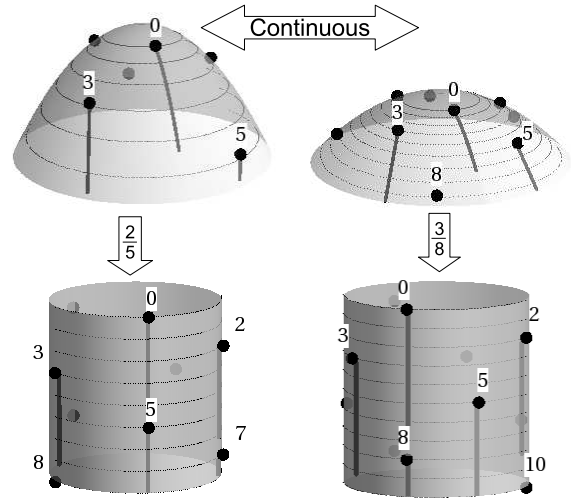


Figure 6: Distinct patterns of  $2/5$  and  $3/8$  orders on the mature stem cylinders (bottom) result from similar arrangements of leaf primordia at the shoot apical meristems (top). Each dot represents a leaf node, through which a dotted line is drawn to demarcate internodes. Leaf traces (line segments) are aligned in a  $2/5$  phyllotaxis pattern if their length is greater than three and less than five internodes (left), whereas a  $3/8$  phyllotaxis results if it is greater than five and less than eight internodes (right).

length represented in internode units. Top two patterns in Fig. 6 represent the initial arrangements of the most common case of  $137.5^\circ$  angular divergence, whereas their growth rates in the radial direction are different, i.e., the two patterns are characterized with different plastochron ratios (Richards (1951)). At this point, the difference is not a qualitative but a quantitative one. Leaf traces (line segments) in the left pattern traverse about four internodes, while those in the right pattern traverse about six internodes. As the figure shows, a qualitative difference is brought about through the quantitative difference in the trace length: geometric constraints tend to achieve either a  $2/5$  or  $3/8$  phyllotaxis on the mature stem depending on whether the trace length is shorter or longer than five internodes. Experimentally, the difference would be judged on whether leaf trace 0 is identified or not in the cross section at the level of node 5. In a similar manner, the threshold value of the trace length for the transition from  $3/8$  to  $5/13$  order is eight internodes, the denominator of the lower order fraction. These are indicated by horizontal dashed lines in Fig. 3, as already remarked. In terms of the threshold length, the phyllotaxis transition is interpreted consistently without resort to operations of elaborate mechanisms like genetic programs; the phyllotaxis transitions are caused because changing length of the leaf trace *happens to* cross the threshold values of five and eight internodes. As illustrated in Fig. 6, this view provides a consistent explanation of empirical observation that large meristems result in arrangements of higher order fractions. Unequal distribution of divergence angle noted in Fig. 4 is

circumstantial evidence of a unique intrinsic angle close to  $137.5^\circ$  and secondary distortions therefrom.

Fibonacci numbers 5 and 8 enter as the threshold values because leaf 0 appears close to leaves 5 and 8 (Fig. 6). This in turn is a mathematical consequence of the golden-mean angle at the apex. Mathematically, any number can be approximated by a common fraction with any assigned degree of accuracy. The greater the denominator, the better the approximation. A fast-converging sequence of approximate fractions is uniquely determined for a given number (Hardy and Wright (1979)). For the golden mean 0.3820, it is  $1/2$ ,  $1/3$ ,  $2/5$ ,  $3/8$ ,  $5/13$ , etc., the main sequence of phyllotaxis. The denominators of these approximate fractions comprise the index differences of nearby leaves, namely the threshold values for the trace length. Thus, the geometric interpretation predicts a correlation between the fraction index of the phyllotaxis order and the trace length represented in internode units. Indeed, it has been remarked as a general rule; the higher phyllotaxis order is associated with the longer leaf trace (Girolami (1953); Esau (1965)). To conclude, the plant in its maturity, as it were, achieves rational approximations to a divergence angle at the apex in conformity with the leaf-trace length in internode units.

Mathematically, the golden mean is the worst “approximable” real number in the sense that the sequence of the approximate fractions converges most badly. In this connection, it has been commonly mentioned, despite objections, that the golden-mean divergence is advantageous because leaves are distributed most evenly to sunlight. When viewed in the context of this study, the golden-mean divergence distributes the leaf traces most efficiently to coordinate the vascular system. Although “phyllotaxis” is the arrangement of leaves on a stem according to dictionaries, the geometric view on the leaf-trace organization, the arrangement of leaves in a stem, may shed a new light on the long-standing problem of phyllotaxis in vascular plants.

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